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Cortical Effects of Shifting Letter Position in Letter Strings of Varying Length

Piers Cornelissen¹, Antti Tarkiainen², Päivi Helenius², and Riitta Salmelin²

Abstract

■ Neuroimaging and lesion studies suggest that occipito-temporal brain areas play a necessary role in recognizing a wide variety of objects, be they faces, letters, numbers, or household items. However, many questions remain regarding the details of exactly what kinds of information are processed by the occipito-temporal cortex. Here, we address this question with respect to reading. Ten healthy adult subjects performed a single word reading task. We used whole-head magnetoencephalography to measure the spatio-temporal dynamics of brain responses, and investigated their sensitivity to: (1) lexicality (defined here as the difference between words and consonant strings), (2) word length, and (3) variation in

letter position. Analysis revealed that midline occipital activity around 100 msec, consistent with low-level visual feature analysis, was insensitive to lexicality and variation in letter position, but was slightly affected by string length. Bilateral occipito-temporal activations around 150 msec were insensitive to lexicality and reacted to word length only in the timing (and not strength) of activation. However, vertical shifts in letter position revealed a hemispheric imbalance: The right hemisphere activation increased with the shifts, whereas the opposite pattern was evident in the left hemisphere. The results are discussed in the light of Caramazza and Hillis's (1990) model of early reading. ■

INTRODUCTION

Cognitive models of reading (e.g., Caramazza & Hillis, 1990) propose a hierarchy of information processing on a continuum from the simple to the increasingly elaborate and abstract. The early components of reading comprise: retinotopically organized visual processing; the extraction of higher-order image properties (i.e., complex features or object-specific properties) within an object-centered framework; and finally, the interface between orthographic/graphemic and phonological processing. Our recent magnetoencephalography (MEG) data on single-word perception have revealed a systematic sequence of activation via basic visual feature processing to object-level analysis in the human occipito-temporal cortex (Helenius, Tarkiainen, Cornelissen, Hansen, & Salmelin, 1999; Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999). In these studies, we used gray-level stimuli consisting of rectangular patches in which single letters, two-letter syllables, or four-letter words, were embedded and to which variable Gaussian noise was added. In addition, we compared letter-string responses with those elicited by symbol strings of an equivalent length. These manipulations dissociated three different response patterns. The first of these, which we call Type I, took place

around 100 msec after stimulus onset. It originated in the vicinity of the V1 cortex and was distributed along the ventral visual stream. This response was systematically modulated by noise but was insensitive to the stimulus content, suggesting involvement in low-level analysis of visual features (Tarkiainen, Cornelissen, & Salmelin, 2002). The second pattern, which we call Type II, took place around 150 msec after stimulus onset and was concentrated in the inferior occipito-temporal region with left hemisphere dominance. This activation was greater for letter strings than for symbol strings, and is likely to reflect an object-level processing stage that acts as a gateway to higher processing areas (Tarkiainen et al., 2002). The third pattern (Type III) also occurred in the time window around 150 msec after stimulus onset, but originated mainly in the right occipital area. Like Type II responses, it was modulated by string length, but showed no preference for letters as compared with symbols.

These data suggest an important role for the inferior occipito-temporal cortex in reading within 200 msec after stimulus onset and are consistent with findings from intracranial recordings (Nobre, Allison, & McCarthy, 1994) and our earlier MEG results (Salmelin, Service, Kiesilä, Uutela, & Salonen, 1996). Nobre et al. (1994) demonstrated letter-string-specific responses bilaterally in the posterior fusiform gyrus about 200 msec after stimulus onset. MEG recordings by Salmelin et al. (1996)

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showed strong transient responses to words and non-words in the bilateral inferior occipito-temporal cortex in fluent readers at 150–200 msec. However, in dyslexic subjects, the left but not right hemisphere response was missing, suggesting a special role for the left inferior occipito-temporal cortex in fluent reading within the first 200 msec after seeing a letter string.

These intracranial and neuromagnetic findings are broadly consistent with results from PET (Rumsey et al., 1998; Price, Moore, & Frackowiak, 1996; Petersen, Fox, Posner, Mintun, & Raichle, 1989; Petersen, Fox, Snyder, & Raichle, 1990) and fMRI (Booth et al., 2002; Puce, Allison, Asgari, Gore, & McCarthy, 1996; Pugh et al., 1996) studies of reading, as well as studies of individuals who have acquired alexia as a result of brain lesions (Henderson, 1986; Damasio & Damasio, 1983; Ajax, 1967). Nevertheless, there are some potential differences. The low-level visual feature analysis and object-level processing stages revealed by neurophysiological recordings would be readily equated with early retinotopically organized visual processing and subsequent extraction of object-specific properties (Caramazza & Hillis, 1990), respectively. However, it is currently not at all clear if the early (neuromagnetic) occipito-temporal activation also reflects access to the visual word form and/or phonological level. Electrophysiological and hemodynamic measures suggest that the occipito-temporal area BA 37 can be involved in phonological processing (Price, 2000; Burnstine, Lesser, Hart, Uematsu, Zinreich, & Drauss, 1990; Luders et al., 1986) and that it may even represent a specialized word form area (see e.g., Leff et al., 2001; Cohen et al., 2000; Brunswick, McCrory, Price, Frith, & Frith, 1999), but it is not clear whether this is the same activation as revealed with MEG studies of reading.

Here we use MEG to explore further the dynamics of single-word reading. We are particularly interested to extend our understanding of Type II (inferior occipito-temporal cortex) brain responses as a function of: (a) letter-string length, (b) the difference between words and random consonant strings, and (c) random vertical shifts of letter position.

Letter String Length

Two recent studies of reading, one using PET (Mechelli, Humphreys, Mayall, Olson, & Price, 2000) and one using fMRI (Indefrey et al., 1997), revealed monotonic increases in signal strength as a function of word length. These effects were visible in the midline posterior occipital cortex, bordering on the fusiform gyrus. Our MEG data (Tarkiainen et al., 1999) also showed increases in both Type I and Type II response amplitudes for single letters, two-letter symbols, and four-letter words. In the current study, we sought word-length effects by comparing the responses to four-, six- and eight-letter words.

Words versus Consonant Strings

Our main aim in this study was to focus on early aspects of letter-string processing. As a simplistic measure of “lexicality,” we compared responses to words versus random consonant strings. It is important to emphasize that this comparison cannot, and was not intended, to distinguish between orthographic, phonological, and semantic components in word recognition. Instead, we were looking for a much simpler distinction. Since written Finnish has a highly transparent orthography, letter strings comprising legal consonant–vowel combinations (whether they are words or pseudowords) are automatically pronounceable; they unavoidably activate the commensurate phonological (\pm semantic) representations. By comparison, random consonant strings cannot do this. Therefore, by comparing word with consonant-string responses, we should be able dissociate those visual processes required to extract orthographic information alone, from those processes related to the interface between orthography and phonological/semantic processing.

Letter-String Shifting

Vertical shifts of letter position are intended to elucidate where and when letter-position information may be encoded. Abstract letter identity, independent of font type and case, is likely to represent the basic perceptual unit of visual word recognition (Grainger & Jacobs, 1996; Besner & McCann, 1987). In order that letter identities can be mapped onto whole-word representations in memory, evidence suggests that we also compute relative letter position (Grainger & Dijkstra, 1995). The behavioral and computational literature (Whitney, 2001; Peressotti & Grainger, 1995, 1999; Humphreys, Evett, & Quinlan, 1990; Mason & Katz, 1976) suggests that relative letter position is most likely computed in an object-centered space that is also invariant for letter size, font, and case. A letter-position code of this kind would therefore be sensitive to the relative difference between “TRIAL” and “TRAIL,” since the two-letter strings differ with respect to the identities of the letters in string positions 3 and 4. But the code would be insensitive to the absolute position of the letter string in the visual field. Historically, letter-position encoding has been investigated behaviorally by using visual priming techniques (Peressotti & Grainger, 1995, 1999; Humphreys et al., 1990). For example, Humphreys et al. (1990) showed that significant positive priming is obtained when prime and target letters respect their relative position in a target string while violating absolute position (e.g., BVK, but not TBVKU facilitates BLACK). Priming techniques of this sort are not ideal paradigms for use with MEG. The typical stimulus sequence: namely, fixation cross, prime string, target string and mask, generates a rapid sequence of

Figure 1. Appearance of four-, six-, and eight-letter words as well as six-letter consonant strings presented linearly or with vertical shifts of letter position.

	Linear strings	Shifted strings
8-letter words	RESURSSI	<div> <div>E</div> <div>R</div> <div>S</div> <div>S</div> <div>S</div> <div>S</div> <div>S</div> <div>I</div> </div>
6-letter words	MAINOS	<div> <div>I</div> <div>M</div> <div>A</div> <div>N</div> <div>O</div> <div>S</div> </div>
4-letter words	LUMI	<div> <div>U</div> <div>L</div> <div>M</div> <div>I</div> </div>
6-letter consonant strings	TNTLLR	<div> <div>N</div> <div>T</div> <div>L</div> <div>L</div> <div>R</div> </div>

transient occipital responses, which may overlap, and this makes it very difficult to model the data satisfactorily. Therefore, to investigate letter-position encoding in the current study, we present an alternative approach that is better suited to MEG because it minimizes the number of confoundable transient signals. Our approach assumes that relative letter-position information is computed in an object-centered spatial framework, but we look for brain responses that are sensitive to absolute spatial position in the visual field. By using an exclusionary criterion in this way, we aim to identify where relative letter-position information is not encoded, instead of where it is encoded. This approach has the advantage that it depends on measuring positive differences between experimental conditions, rather than identifying null effects. Thus, for example, random vertical shifts of the constituent letters within a word should modulate spatial processes that are sensitive to absolute position as compared with linearly printed words. But since the same manipulation nevertheless preserves the relative order of the letters within a word, there should be no effect on those components in the reading network that are primarily sensitive to relative letter position—these should show vertical shift invariance.

In summary, as illustrated in Figure 1, we used whole-head MEG to measure the spatio-temporal dynamics of brain responses, and investigated their sensitivity to the following letter-string parameters: (1) lexicality, (2) word length, and (3) variation in letter position.

RESULTS

Behavioral Data

A number of investigators have explored the effects of text mutilation both behaviorally and with neuroimaging

techniques (e.g., Polk & Farah, 2002; Dickerson, 1999; Bock, Monk, & Hulme, 1993; Paap, Newsome, & Noel, 1984; Coltheart & Freeman, 1974). The form of the mutilation has usually involved mixing upper- with lower-case letters (e.g., hOnEy) or manipulating interletter spacing. There appears to be no previous report of vertical letter shifting as used here. For this reason, we describe briefly the results of a behavioral experiment using this manipulation to demonstrate that there is indeed an increase in vocal reaction time (vRT) to words containing vertical letter-position shifts compared to linearly presented words.

Six adult subjects each read aloud 120 six-letter Finnish nouns which appeared on screen for 100 msec. Forty words were presented in the normal linear fashion; 40 words had either letters 2 and 3 or 3 and 4 displaced by a half-letter height; 40 words had either letters 2 and 3 or 3 and 4 displaced by a whole-letter height. The order of stimulus presentation was randomized for each subject. vRTs were recorded and distributions of reaction times for each participant were individually inspected. To remove the influence of outlying data points, we applied a relatively conservative criterion by clipping individual distributions for each subject for each condition at their tenth and ninetieth percentiles (Ratcliff, 1993; Miller, 1991).

Figure 2 shows mean vRT plotted as a function of the magnitude of vertical letter shift: no shift (mean vRT 557 msec, *SEM* 3.2), half-letter height (mean vRT 562 msec, *SEM* 3.5) or whole-letter height (mean vRT 572 msec, *SEM* 3.3). The effect of this manipulation is most marked for the whole-letter height condition. A one repeated-measures ANOVA of vRTs showed a significant main effect of shift, $F(2,10) = 8.5$, $p < .01$. Post hoc tests (Tukey's HSD, $\alpha = .05$, critical difference = 3.8 msec) showed that this was attributable to statistically significant differences between

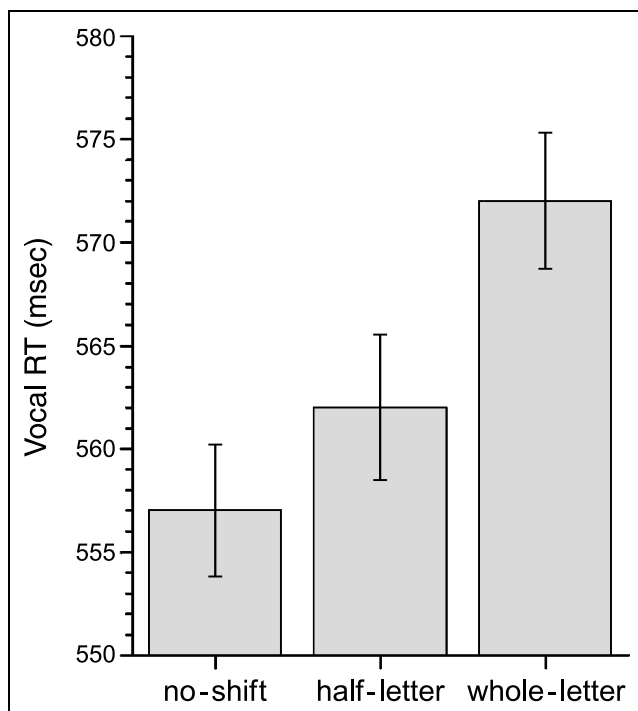


Figure 2. Bar charts of mean vocal reaction times in a single-word reading task plotted as a function of the size of vertical letter shift.

whole-height and half-height shifts as well as between whole-height and no-shift.

MEG Data

Equivalent current dipoles (ECDs) representing active source areas were determined using the data from a minimum of six sensor pairs surrounding the local magnetic signal maximum, at time points when visual inspection revealed clear dipolar field patterns with minimum interference from other active brain areas. The magnetic field variation was accounted for by 8 to 13 source areas in each subject. Since the active source areas were similar across the different stimulus conditions, we were able to select a single set of ECDs for each subject and compile these into a multidipole model. To characterize the time course of activation in each of these cortical areas as a function of stimulus condition, we then carried out a source waveform analysis. To do this, ECD locations and orientations were kept fixed while their amplitudes were allowed to vary as a function of time in order to best account for the signals measured by all gradiometers.

We analyzed the ECD amplitudes and latencies within and across experimental conditions in two ways: (1) region of interest (ROI) and (2) criterion search. The first approach is based on our previous work (Tarkiainen et al., 1999) and is aimed at further characterizing the properties of Type I and Type II source behavior. The second approach is inspired by the fact that the network of activity induced by single-

word reading is extensive, and we wanted a means of applying a widespread search throughout the brain to look for effects of our three manipulations: lexicality, string length, and shifting letter position.

ROI Analysis

According to Tarkiainen et al. (1999), Type I sources were systematically modulated by noise and Type II sources gave stronger responses to words than symbol strings. Since none of the present stimuli were masked in noise, nor did the stimulus set contain symbol strings, classification of Type I and Type II activity was not possible according to the criteria of Tarkiainen et al. However, since the source distributions and latencies were similar in both studies, we decided to use the time and location information given by Tarkiainen et al. to identify “candidate” Type I (cType I) and “candidate” Type II (cType II) sources in this study.

cType I Sources

cType I sources fulfilled the following selection criteria: (1) sources had to be located around the midline of the occipital cortex; (2) sources had to be active before 130 msec; (3) peak amplitude had to exceed $1.96 \times$ standard deviation of prestimulus baseline (-200 to 0 msec). Finally, to minimize the repeated-measures problems inherent in selecting an unequal number of sources per subject, where there were two or more potential cType I sources, we selected the one which had the earliest latency. Defined in this way, 10/10

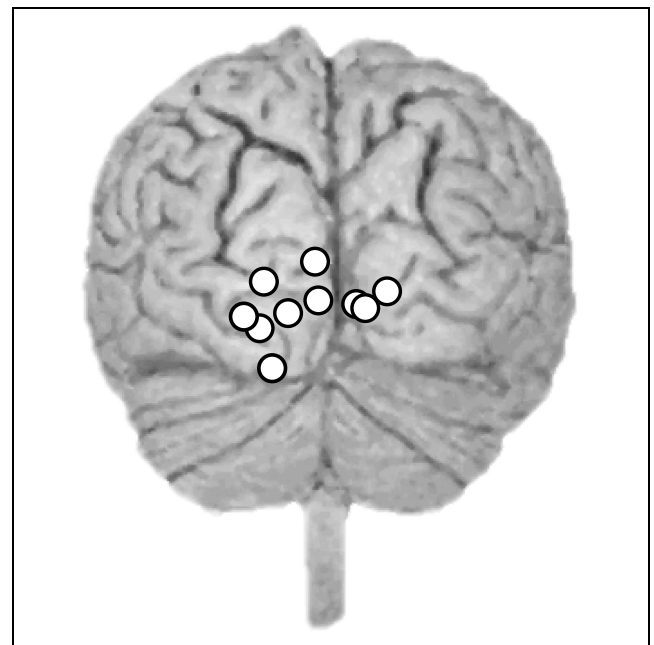


Figure 3. Locations of the 10 cType I sources (one source per subject). All sources are mapped onto the same brain and projected to the surface.

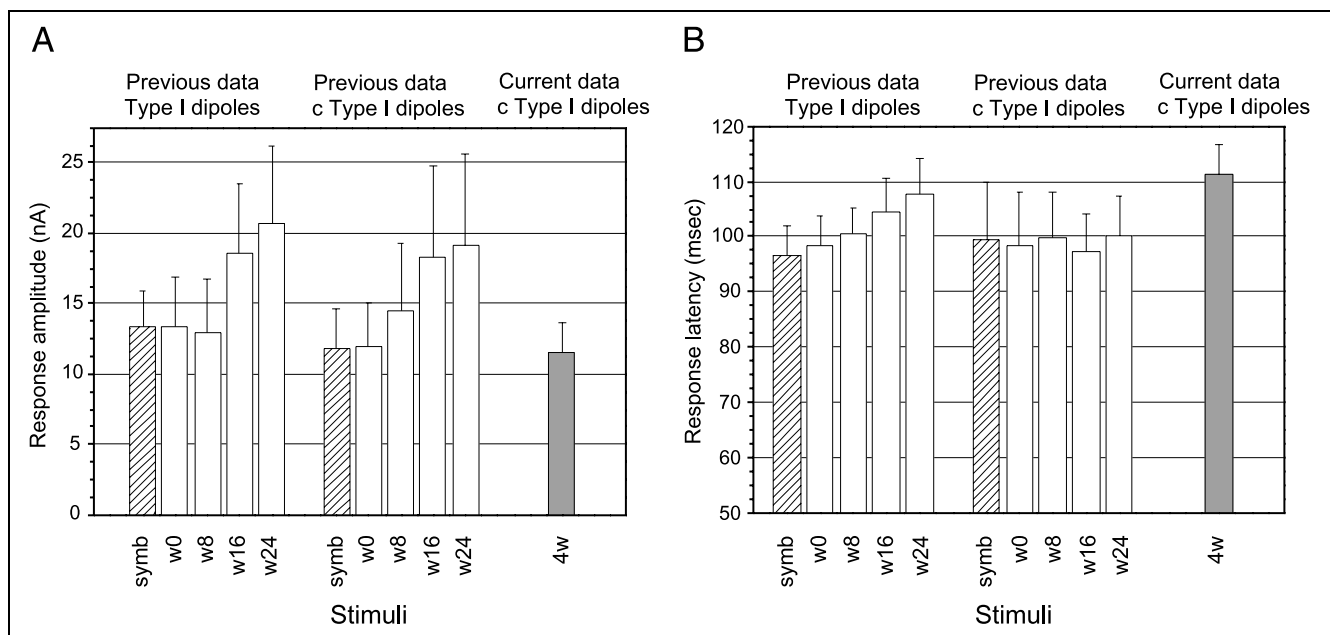


Figure 4. Bar charts of mean source amplitude (A) and latency (B) of Type I and cType I sources. The data are plotted as a function of stimulus condition: symb = symbol string; w0, w8, w16, and w24 = words embedded in Gaussian noise at one of four levels (0, 8, 16, and 24); 4w = normally printed, four-letter words. Error bars represent one standard error of the mean.

subjects showed early midline occipital activity with 3/10 subjects having two sources active in this region. Figure 3 displays the resultant population of cType I sources mapped onto one brain, and projected to its surface.

Comparison of cType I and Type I Sources Using the Dataset of Tarkiainen et al. (1999)

Six of the 10 subjects in the current study also took part in our original investigation of the dynamics of letter-

string processing (Tarkiainen et al., 1999). We tested whether the behavior of our cType I sources (modeled from the current dataset) corresponded to the behavior of Type I sources in Tarkiainen et al. Therefore, for these 6 subjects, we fitted the complete dipole models derived from the current dataset to the field patterns of the earlier dataset. We then compared these cType I responses to the original Type I responses. This strategy was only feasible because the stimuli, cortical activation patterns, and our resultant source models were highly similar between the two studies.

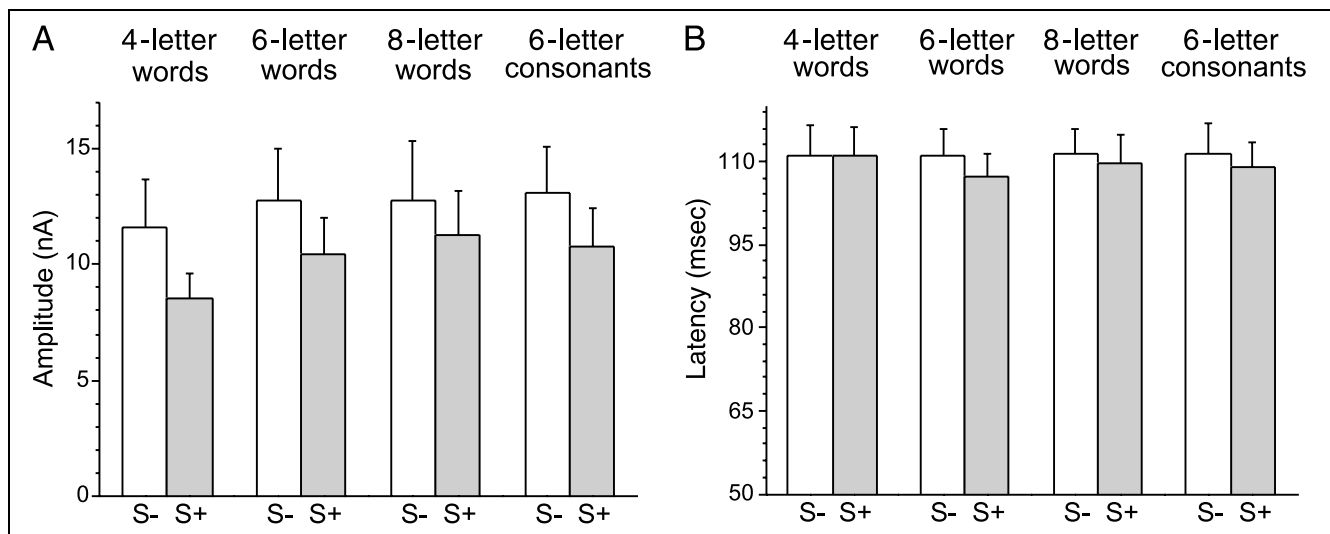


Figure 5. Bar charts of mean source amplitude (A) and latency (B) of cType I sources. The data are plotted as a function of stimulus condition: four-, six-, eight-letter words and six-letter consonant strings. Light bars (S-) represent responses to linear letter strings. Dark bars (S+) represent responses to shifted letter strings. Error bars represent one standard error of the mean.

Figure 4A and B shows the average peak amplitudes and peak latencies of Type I and cType I sources to four-element geometric symbols (i.e., circle, square, triangle, diamond, with no noise added), and four-letter words embedded in one of four levels of 2-D Gaussian noise (0, 8, 16, or 24). In addition, to ease comparison between the two studies in which we used different MEG recording devices and stimulus presentation equipment, we also include the mean peak amplitude and latency of cType I responses to linear four-letter words from the current dataset. In all cases, error bars represent 1 standard error of the mean.

To compare Type I and cType I sources, we ran one between groups (Factor 1, study: previous, current), one repeated-measures (Factor 2, stimulus: symbols, w0, w8, w16, w24) ANOVAs of response amplitude and latency. The model for amplitude revealed a significant effect of stimulus condition, $F(4,40) = 5.6$, $p < .005$, and a nonsignificant effect of study, $F(1,10) = .32$, $p > .5$. The two-way interaction, Condition by Study, was also nonsignificant, $F(4,40) = .62$, $p > .5$. This suggests that our cType I sources are statistically indistinguishable from Type I sources in the Tarkiainen et al. (1999) study. Specifically, while there was no differential response between symbol and letter strings, addition of noise to four-letter words caused a monotonic increase in response amplitude. For latency, there were no significant main effects or interactions between condition and study. Therefore, we accept that the present selection of cType I sources corresponds, with reasonable accuracy, to the original Type I sources in Tarkiainen et al.

Behavior of cType I Sources in the Current Dataset

Figure 5A and B shows the mean peak amplitudes and latencies for cType I sources in response to linear and shifted four-, six- and eight-letter words and six-letter consonant strings. “S–” represents linear letter strings and “S+” represents shifted letter strings. Figure 5A and B shows that there are negligible effects of word length, lexicality (i.e., words vs. consonants), and vertical shifts of letter position on both the peak amplitude and peak latency of cType I responses. These impressions were confirmed quantitatively by two repeated-measures ANOVAs (Factor 1, letter string: 4w, 6w, 8w, 6c; Factor 2, shift: present, absent) of peak amplitude and latency. There were no significant (at $p < .05$) main effects or interactions for either the amplitude or the latency data.

cType II Sources

cType II sources fulfilled the following selection criteria: (1) all potential cType I sources were excluded; (2) cType II sources had to be located preferentially in the inferior occipito-temporal cortex; (3) cType II sources had to be active before 200 msec; (4) peak activity had to exceed 1.96 times the standard deviation of baseline.

This rendered at least one source per hemisphere per person; 3/10 subjects had two and 1/10 subjects had three potential cType II sources for the left hemisphere and/or the right hemisphere. For reasons of statistical independence, we selected just one left hemisphere and one right hemisphere source per subject. If there was a choice to be made between potential cType II sources, we selected the one with the earliest latency. Finally, in one subject, it was difficult to fulfil criterion 2, since the RH cType II source was midline rather than lateral and inferior. For the sake of a balanced analysis, we relaxed the spatial criterion. These procedures rendered 10 left occipito-temporal sources, and 10 right occipito-temporal sources as in Figure 6.

Comparison of Activations of Left Hemisphere and Right Hemisphere cType II Sources with Type II Sources, Using the Previous Data (Tarkiainen et al., 1999)

In our previous study (Tarkiainen et al., 1999), the Type II sources, defined by their preferential responses to letter strings, were centered on the left inferior occipito-temporal cortex. In the same 6 subjects who took part in both studies, we now fitted the complete multidipole models from the current study to the field patterns from the previous study. We then compared the behavior of the current population of left hemisphere cType II and right hemisphere cType II sources with the Type II sources from the previous study.

Figure 7A and B shows average peak amplitudes and latencies for responses to four-element geometric symbols (e.g., circle, square, triangle, diamond), and

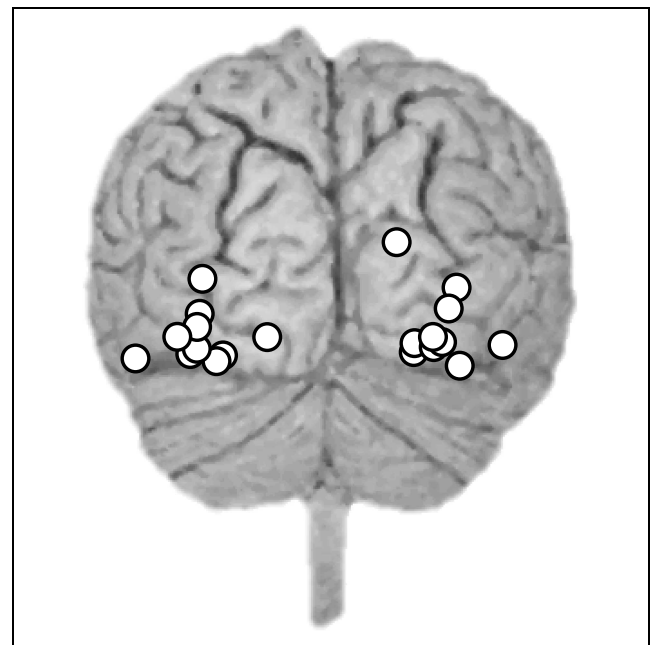


Figure 6. Locations of the 10 left hemisphere cType II and 10 right hemisphere cType II sources (one source per subject per hemisphere). All sources are mapped onto the same brain and projected to the surface.

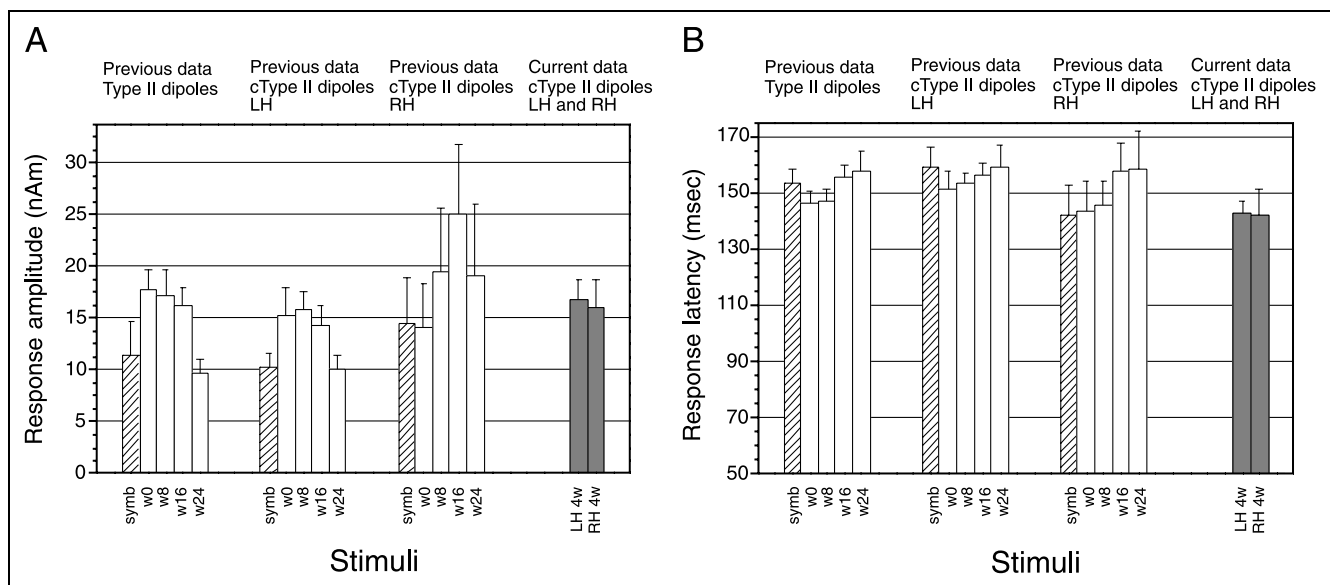


Figure 7. Bar charts of mean source amplitude (A) and latency (B) for Type II, left hemisphere cType II and right hemisphere cType II sources. The data are plotted as a function of stimulus condition: symb = symbol string; w0, w8, w16, and w24 = words embedded in Gaussian noise at one of four levels (0, 8, 16, and 24); 4w = normally printed, four-letter words; LH and RH = left and right hemispheres, respectively. Error bars represent one standard error of the mean.

four-letter words embedded in one of four levels of 2-D Gaussian noise (0, 8, 16, or 24). In addition, to compare amplitude and latency of responses from the two studies, the left hemisphere and right hemisphere amplitudes are given for cType II responses to linear four-letter words, calculated from the current dataset.

For both Type II and left hemisphere cType II sources, four-letter words gave stronger responses than four-element symbol strings in the absence of Gaussian noise. These responses collapsed at the highest noise level where reduced visibility made letter identification extremely difficult. These findings were confirmed quantitatively by one between-groups (Factor 1, study: previous, current), one repeated-measures (Factor 2, stimulus: symbols, w0, w8, w16, w24) ANOVAs of response amplitudes and latencies. For amplitude, we found a significant effect of stimulus condition, $F(4,40) = 10.5$, $p < .0005$, and a nonsignificant effect of study, $F(1,10) = 1.1$, $p > .1$. The two-way interaction Condition by Study was also nonsignificant, $F(4,40) = 0.13$, $p > .5$. For latency, we found a significant effect of stimulus condition, $F(4,40) = 3.15$, $p < .05$, and a nonsignificant effect of study, $F(1,10) = .32$, $p > .5$. The two-way interaction Condition by Study was also nonsignificant, $F(4,40) = 0.29$, $p > .5$. This result shows that left hemisphere cType II sources from the current study gave responses that were statistically indistinguishable from those of the Type II sources in Tarkiainen et al. (1999). Thus, as suggested in that article, the early left hemisphere occipito-temporal activity in reading tasks may generally be concerned with processing letter strings or at least letter-like objects.

In contrast, right hemisphere cType II sources behaved differently to Type II and left hemisphere cType II

sources. Right hemisphere cType II responses to four-letter words and four-element symbol strings were indistinguishable. Moreover, even the noisiest words gave stronger responses than noise-free symbol strings and noise-free words. We ran additional one between-groups (Factor 1, hemisphere: left, right), one repeated-measures (Factor 2, stimulus: symbols, w0, w8, w16, w24) ANOVAs of amplitudes and latencies to compare left hemisphere cType II and right hemisphere cType II responses. For amplitude, only the main effect of stimulus and the two-way interaction Hemisphere by Stimulus were significant, $F(4,40) = 8.9$, $p < .0005$, and $F(4,40) = 5.9$, $p < .0005$, respectively. For latency, only the main effect of stimulus was significant, $F(4,40) = 3.1$, $p < .05$. These findings strongly suggest that, within 200 msec poststimulus, right hemisphere occipito-temporal sources (or at least right hemisphere cType II sources) respond differently, but in parallel to left hemisphere occipito-temporal sources, and that they do not show preferential activation for letter strings.

Behavior of Left Hemisphere and Right Hemisphere cType II Sources in the Current Dataset

Figure 8A and B illustrates the mean peak amplitudes and peak latencies, respectively, for all 10 left hemisphere and all 10 right hemisphere cType II source responses, evoked by four-, six-, and eight-letter words, as well as six-letter consonant strings. In Figure 8A and B, responses to shifted letter strings are indicated by “L+” and “R+” in the left hemisphere and right hemisphere, respectively. Responses to linear letter strings are indicated as “L–” and “R–” in the left hemisphere and right hemisphere, respectively. Figure 8A shows a

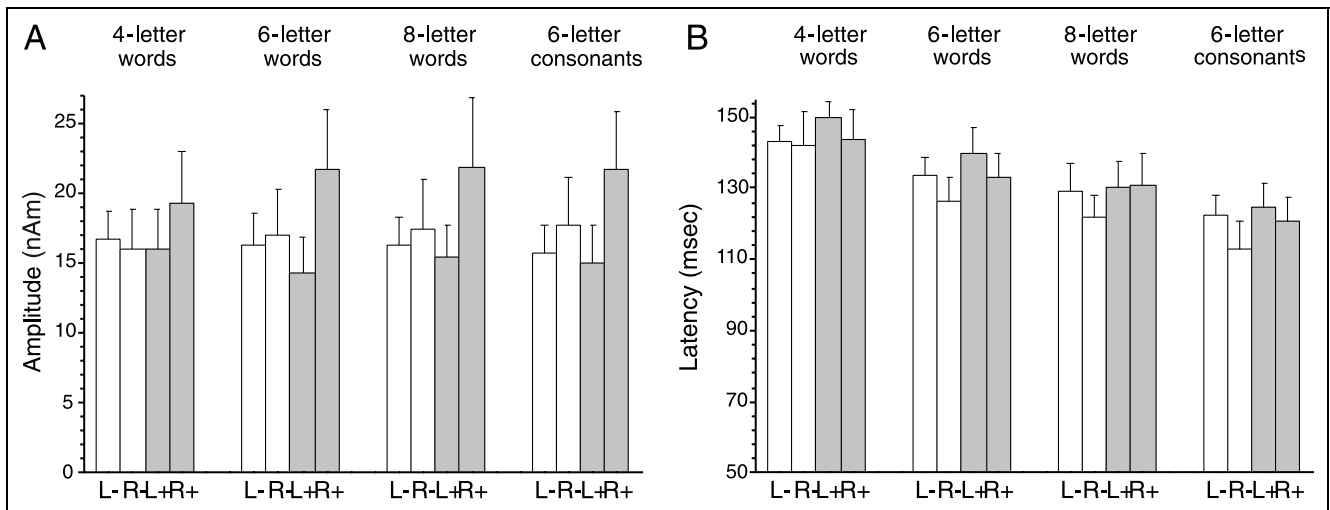


Figure 8. Bar charts of mean source amplitude (A) and latency (B) of cType II sources. The data are plotted as a function of stimulus condition: four-, six-, eight-letter words and six-letter consonant strings. Light bars (L– and R–) represent responses to linear letter strings in the left and right hemispheres, respectively. Dark bars (L+ and R+) represent responses to shifted letter strings in the left and right hemispheres, respectively. Error bars represent one standard error of the mean.

specific increase (~25%) in amplitude of right hemisphere activity when letter strings were shifted. However, no other effects of string length or lexicality are apparent. Quantitatively, this was confirmed by repeated-measures ANOVAs of peak response amplitudes (Factor 1, shift: present, absent; Factor 2, letter string: 4w, 6w, 8w, 6c). While the analysis of left hemisphere amplitudes revealed no significant main effects or interactions, the same analysis of right hemisphere amplitudes revealed a significant main effect of shift, $F(1,9) = 5.34, p = .05$ (i.e., RH amplitudes were elevated by randomly shifting letter position).

Figure 8B shows the differential effects of letter-string type on response latencies. The most obvious effect

is that increasing string length was associated with a small (up to 20 msec) reduction in response latency. Repeated-measures ANOVAs of peak response latency (Factor 1, shift: present, absent; Factor 2, letter string: 4w, 6w, 8w, 6c) showed, for the left hemisphere, significant main effects of letter string and shift, $F(3,27) = 22.4, p < .0005$ and $F(1,9) = 14.00, p < .005$. For the right hemisphere, only the main effect of letter string was significant, $F(3,27) = 11.4, p < .0005$.

Criterion Searches

Figure 9 shows all source locations from all subjects mapped onto one brain, and projected to its surface

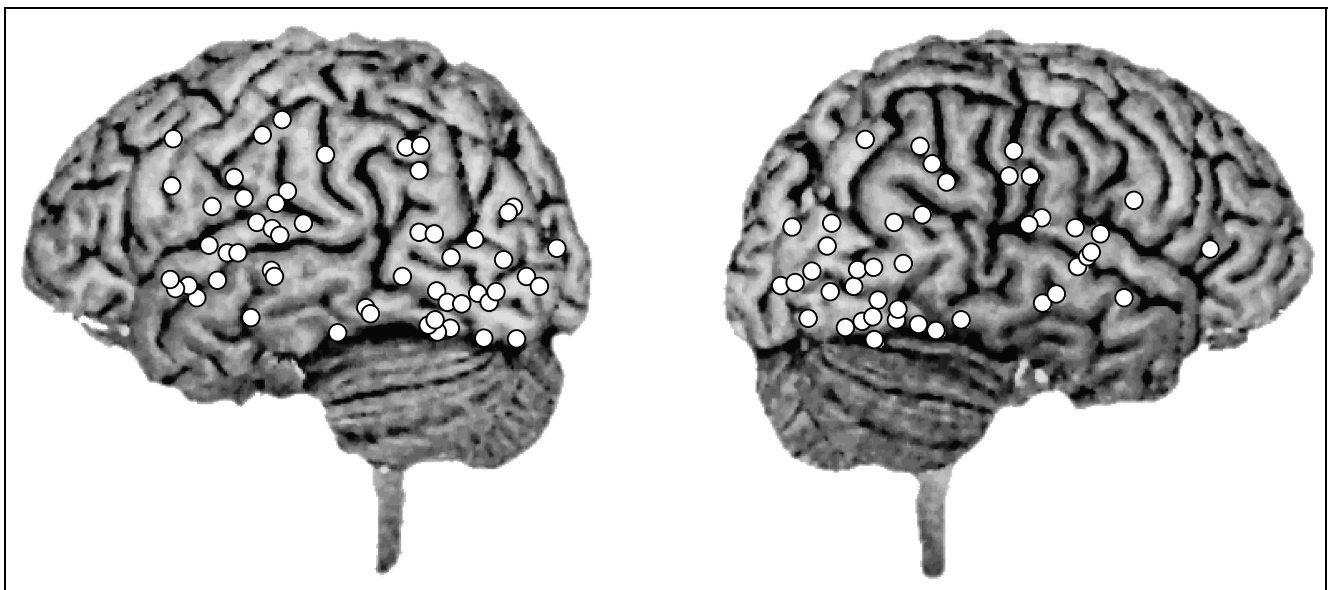


Figure 9. Location of all sources (see main text for details).

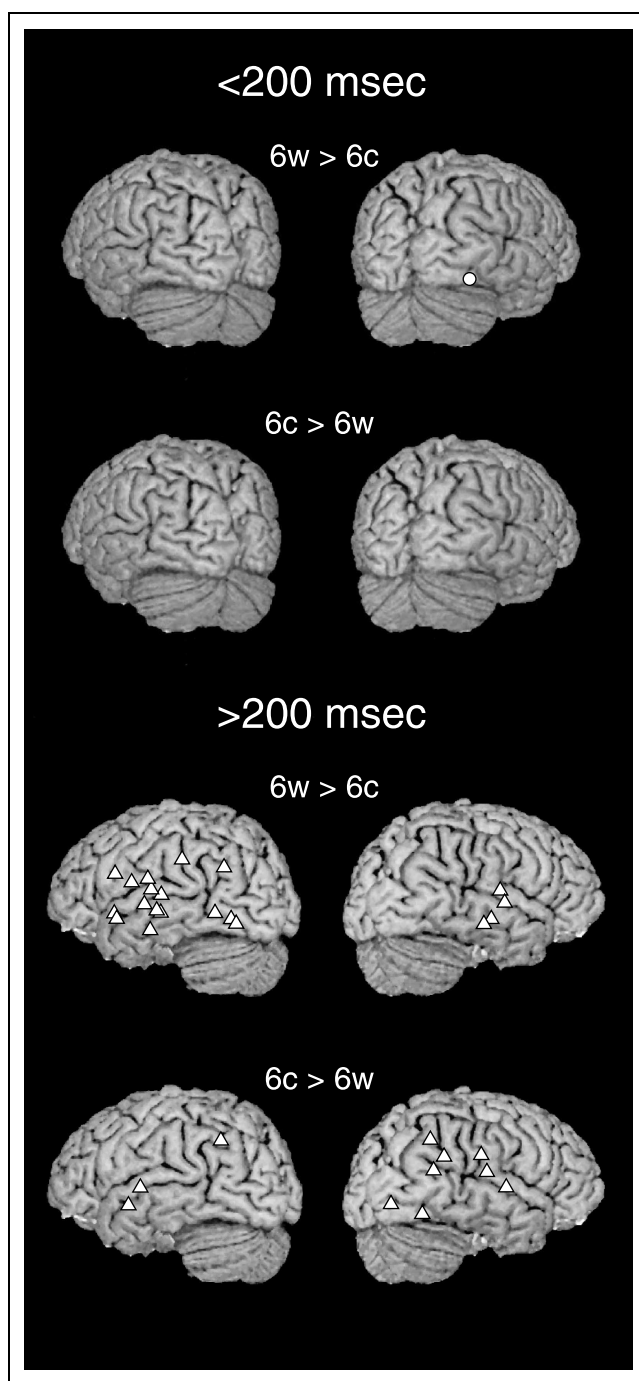


Figure 10. Location of sources that fulfil the criteria for the lexicity effect. Sources in the left (LH) and right (RH) hemispheres are shown separately. The first two rows represent sources which were active before 200 msec after stimulus onset (circles). The second two rows represent sources that were active later than 200 msec after stimulus onset (triangles). 6w = six-letter words, printed normally; 6c = six-letter consonant strings, printed normally.

for illustration. Left and right hemisphere views are shown separately.

The extensive spatial distribution of these sources illustrates the complex and widespread activity evoked by the experimental tasks. Our aim in conducting the criterion searches was to find sources that showed clear

responses to lexicity, letter string length, and letter-position shifting. From a sampling point of view, this approach is less statistically rigorous than the ROI analysis, since it does not permit balanced analyses. For example, one subject may have two or more sources that satisfy a particular criterion, whereas another subject may have none. Nevertheless, by loosening the stringency of the source selection, it is possible to obtain a better overview of the activity patterns we found.

We selected those comparisons that were expected to show the clearest differences: for string length, four-letter words versus eight-letter words; for the shift effect, shifted eight-letter words versus linear eight-letter words; for lexicity, six-letter words versus six-letter consonant strings. For all comparisons before 200 msec, a difference between peak amplitudes was considered significant if it exceeded 1.96 times the baseline standard deviation. For all comparisons after 200 msec, a difference between conditions had both to exceed 1.96 times the baseline standard deviation and persist for at least 100 msec. The reason for the second requirement is that, unlike early activations, later activations tend not to show clear maxima. Such prolonged activation cannot be captured by simple peak parameters.

Lexicity Effects

Figure 10 illustrates the distribution of sources that satisfied criteria for lexicity effects. Before 200 msec, only 1/10 subjects showed a single source satisfying the criterion for 6w > 6c. However, after 200 msec, 10/10 subjects showed at least one source which satisfied the criterion for 6w > 6c. In addition, 8/10 subjects showed at least one source which satisfied the criterion for 6c > 6w. Table 1 below shows the 2 × 2 contingency table for the lexicity criterion search after 200 msec. A Fisher's Exact Test of association for Table 1 was significant at $p < .005$.

Binomial tests then confirmed that lexicity effects did not appear before 200 msec after stimulus onset, and that after 200 msec, subjects were more likely to give stronger responses to six-letter words than six-letter consonants in the left hemisphere ($p < .002$).

Letter-String Length Effects

Figure 11 illustrates the distribution of sources that satisfied criteria for string-length effects. Table 2 summarizes how the sources are distributed. Before 200 msec,

Table 1. Hemisphere versus Six-Letter Consonant Strings and Words

	6c > 6w	6w > 6c
Left hemisphere	3	16
Right hemisphere	8	4

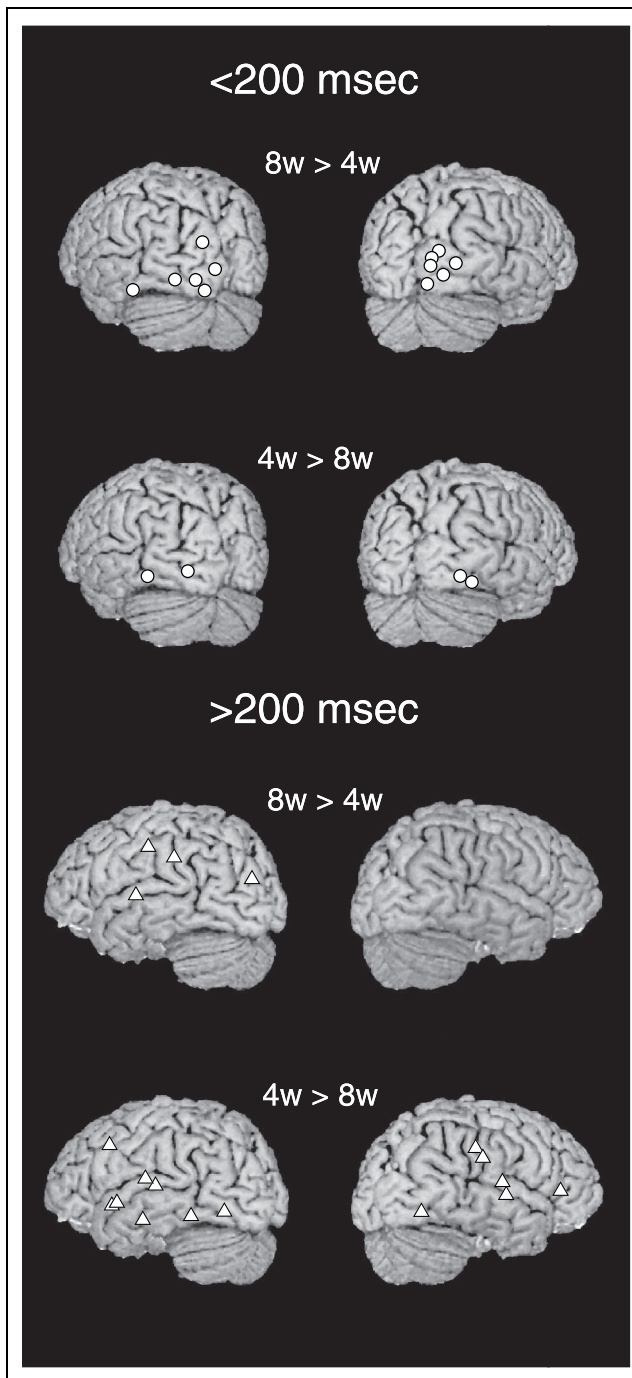


Figure 11. Location of sources that fulfill the criteria for the letter-string length effect. Sources in the left (LH) and right (RH) hemispheres are shown separately. The first two rows represent sources which were active before 200 msec after stimulus onset (circles). The second two rows represent sources that were active later than 200 msec after stimulus onset (triangles). 8w = eight-letter words, printed normally; 4w = four-letter words, printed normally.

8/10 subjects showed at least one source satisfying the criterion for 8w > 4w. After 200 msec, 8/10 subjects showed at least one source which satisfied the criterion for 4w > 8w.

We carried out three Fisher's Exact Tests for the three 2×2 contingency tables shown in Table 2a and b. Only

the test for Table 2b was significant ($p = .005$). These results suggest that neither before nor after 200 msec were subjects likely to show differential hemispheric effects related to letter-string length. However, before 200 msec, subjects were more likely to give stronger responses to eight- than four-letter words (binomial test, $p < .04$). Yet after 200 msec, the reverse was true; subjects were more likely to give stronger responses to four- than eight-letter words ($p < .02$).

Letter-String Shift Effects

Figure 12 illustrates the distribution of sources that satisfied the criteria for shift effects. Before 200 msec, 9/10 subjects showed at least one source satisfying the criterion for 8ws > 8w, and 8/10 subjects showed at least one source satisfying the criterion for 8w > 8ws. After 200 msec, 8/10 subjects showed at least one source satisfying the criterion for 8ws > 8w. We carried out Fisher's Exact Tests for the three 2×2 contingency tables in Table 3a and b.

Table 3a suggests that before 200 msec, subjects were more likely to give stronger responses to linear than shifted eight-letter words in the left hemisphere (binomial test, $p < .02$). Conversely, they were also more likely to give stronger responses to shifted than linear eight-letter words in the right hemisphere ($p < .05$). Fisher's Exact Test for this association was significant ($p = .003$). After 200 msec, no hemispheric differences for the shift effect were detected.

DISCUSSION

In this study, we used MEG to investigate the impact of three variables in a single-word reading task: (a) word length, (b) letter-string lexicality, and (c) random vertical shifts of letter position. In addition, to facilitate the comparison with our previous research in this area, we

Table 2. Distribution of Sources

(a) Before and after 200 msec, letter-string length versus hemisphere

	<200 msec		>200 msec	
	4w > 8w	8w > 4w	4w > 8w	8w > 4w
Left hemisphere	2	6	8	4
Right hemisphere	2	6	6	0

(b) Letter-string length versus time period

	4w>8w	8w>4w
<200 msec	4	12
>200 msec	14	4

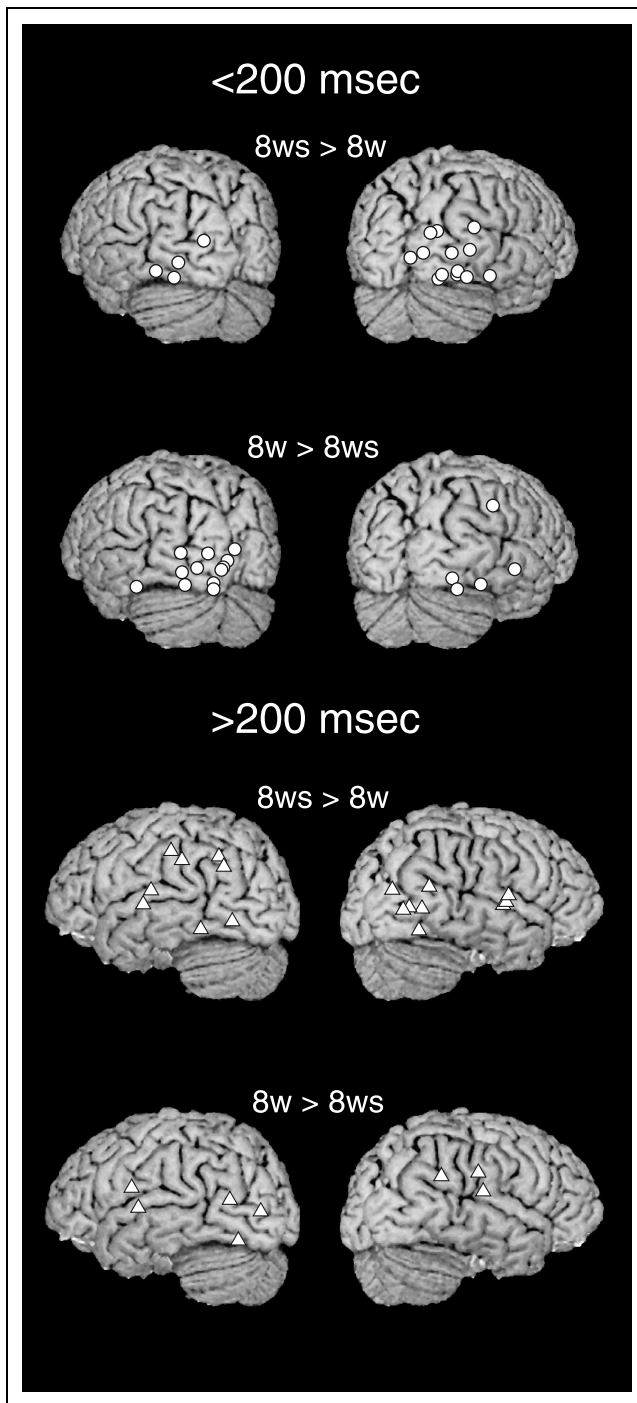


Figure 12. Location of sources that fulfil the criteria for the shift effect. Sources in the left (LH) and right (RH) hemispheres are shown separately. The first two rows represent sources which were active before 200 msec after stimulus onset (circles). The second two rows represent sources that were active later than 200 msec after stimulus onset (triangles). 8w = eight-letter words, printed normally; 8ws = eight-letter words, shifted.

fitted the multipole models derived from the current dataset to the data from an earlier study (Tarkiainen et al., 1999). We argue that this was an extremely stringent test of our current approach to multipole modeling because, as this procedure generated similar

results between the two studies (separated by 2 years), it suggested a high degree of repeatability across time, subjects, measurement devices, methods of analysis, and subtle variation in stimulus presentation.

Effects of Letter-String Length

In the ROI analysis (cType I and cType II sources), we found no significant length effects in activation strengths. The latencies of the more lateral cType II sources showed a small but significant reduction with increasing string length. This “inverted progression” is a continuation of a trend found in our previous study (Tarkiainen et al., 1999): Type II source latencies for single letters, two-letter syllables, and four-letter words were about 156, 149, and 143 msec, respectively.

The criterion search, however, did reveal early (before 200 msec) sources bilaterally around the occipital midline in 8/10 subjects that were stronger for eight-letter than four-letter words. The mean latency of these responses was 125 and 131 msec, respectively. The location and timing closely resemble those characteristic of Type I responses (Tarkiainen et al., 1999, 2002). The apparent discrepancy between the ROI analysis and criterion search requires some consideration.

The effect of string length on the midline occipital (Type I) activity was not expected to be particularly strong for the stimuli used in the present study. Tarkiainen et al. (2002) have shown that the strongest determinant of Type I activation is the visual complexity of a stimulus image. Complexity is defined as follows. Each image is represented by an $M \times N$ matrix, where M is the height of the image and N is the width of the image in pixels. Each matrix element gives the grayscale value of the corresponding pixel. For all image matrices belonging to the same stimulus category, we calculate the column-wise standard deviations of grayscale values and use the mean value to represent that stimulus category. Defined in this way, the larger the complexity

Table 3.

(a) Before and after 200 msec, letter-string shift versus hemisphere

	<200 msec		>200 msec	
	8ws < 8w	8ws > 8w	8ws < 8w	8ws > 8w
Left hemisphere	13	4	5	8
Right hemisphere	5	13	3	9

(b) Letter-string shift versus time period

	8w > 8ws	8ws > 8w
<200 msec	18	17
>200 msec	8	17

of a stimulus image, the greater is the probability of finding a marked contrast difference between adjacent pixels. For face, object, and letter stimuli, we obtained a strong correlation ($r = .97$, $p < .00001$) between the mean peak amplitudes of Type I sources and the mean complexities of the corresponding stimuli (Tarkiainen et al., 2002). The complexity values for the current (linear letter string) stimuli are 5 and 10 for four- and eight-letter words, respectively. In comparison with Tarkiainen et al. (1999), stimulus complexity values were about 5 and 10 for single letters and two-letter syllables respectively, whereas the four-letter words had a complexity of about 20. Moreover, it was the difference between two-letter syllables and four-letter words that showed the greatest change in Type I response amplitude, corresponding to the greatest change in stimulus complexity (letter sizes were different between the two studies, hence the differences in complexity values). Only a very small effect of length in Type I activity was thus expected for the present stimuli. The temporally unlimited criterion search revealed even this small effect in the midline occipital cortex. Significance was not, however, reached for the subgroup of earliest cType I sources which were selected for the ROI analysis. A length effect around the occipital midline is in agreement with hemodynamic data of Mechelli et al. (2000) and Indefrey et al. (1997).

It is noteworthy that not even the criterion search suggested length effects in activation patterns reminiscent of the Type II response. In Tarkiainen et al. (1999), the amplitude of Type II activity increased from single letters to two-letter syllables and further to four-letter real words. It thus seems that when the letter strings are complete words or even nonwords with a typical word length, the exact number of letters no longer has an effect on the strength of the occipito-temporal activation.

Effects of Letter-String Lexicality

The ROI analysis showed that cType I and cType II responses did not discriminate between six-letter words and six-letter consonants. This null result suggests that both cType I and cType II responses are prelexical. It is also consistent with the idea (Tarkiainen et al., 2002) that cType II responses reflect an object-level processing stage that is required for extracting orthographic information, but which is not synonymous with the processing expected of a visual word form area.

The criterion searches did reveal sources whose responses to six-letter words were significantly stronger than those to six-letter consonants. These sources were located predominantly in the left hemisphere, but were only active later than 200 msec after stimulus onset; they were clustered around the peri-sylvian cortex: namely, prefrontal dorsolateral, premotor inferior frontal, superior temporal, and middle temporal areas.

These locations are very similar to the MEG study of Salmelin et al. (1996), in which responses both to nonwords as well as random letter strings were compared to those from words. In their fMRI study, Pugh et al. (1996) also looked for voxels in which the BOLD signal for words was significantly greater than that for consonant strings. The cortical regions in which they found such voxels are very similar to those revealed by our criterion search. Finally, in a recent combined fMRI and ERP study of reading, Cohen et al. (2000) could not distinguish consonant string from word responses until 240 to 360 msec after stimulus onset. Thus, we conclude that since our paradigm is sensitive enough to distinguish brain responses to words from brain responses to consonant strings, the early (before 200 msec) activity in the occipital and inferior occipito-temporal cortex is indeed prelexical.

Effects of Letter-String Shifting

Both the ROI analyses and the criterion searches suggest that sources in the occipito-temporal cortex are sensitive to vertical shifts of letter position within 200 msec of stimulus presentation. In the left hemisphere, we found occipito-temporal sources that gave stronger responses to linear than shifted words (criterion search). In the right hemisphere, both the ROI analysis (cType II sources) and the criterion search suggest that the occipito-temporal cortex responds more strongly to shifted than linear letter strings.

These results are consistent with our original hypothesis: If relative letter position information is computed in an object-centered spatial framework, as suggested by the behavioral and computational literature, then the component(s) in the reading network which carry out this computation should show vertical shift invariance. Therefore, by exclusion, any component in the network that is sensitive to such manipulation is unlikely to be involved in this computation. We found that early (before 200 msec) processing of letter strings in the occipito-temporal cortex appears to be sensitive to vertical letter shifting, which suggests that relative letter-position information is most likely computed elsewhere.

Another factor which may have contributed to these findings is that vertical shifts of letter position disturb the normal balance between local (left hemisphere) versus global (right hemisphere) processing of single words. This is consistent with the findings of Fink, Dolan, Halligan, Marshall, and Firth (1997) and Fink, Halligan, et al. (1997), who investigated the functional anatomy involved in sustaining or switching visual attention between different perceptual levels. Fink, Halligan, et al. used hierarchically organized letters or "Navons" (i.e., large letters made out of small letters) in both a directed attention and a divided attention task. In the former condition, which was intended to reveal

the network involved in stimulus processing, subjects attended to either the local or the global stimulus level. In the latter condition, which was intended to reveal the network involved in controlling attention *per se*, subjects were required to switch attention between local and global levels. Relevant to the current study, global stimulus processing in the directed attention condition involved the right hemisphere prestriate visual cortex, while local stimulus processing involved the left hemisphere prestriate visual cortex. Certainly, it is likely that our subjects would have needed to consciously expand their perceptual span for reading (Rayner, 1998) in the vertical direction. Such a strategy may have emphasized the global processing requirement of the shifted letter strings, thereby altering the balance between left and right occipito-temporal cortical activity.

General Discussion

The first systematic pattern of activity seen in our earlier letter-string studies (Helenius et al., 1999; Tarkiainen et al., 1999) took place in the midline occipital cortex around 100 msec after stimulus onset. Similar activity was observed also in the present study. This activation pattern has been shown to increase with visual complexity of the stimuli (Tarkiainen et al., 2002). In accordance with this view, the present study showed that this processing stage was insensitive to lexicality and vertical shifts of letter position but reacted moderately to word length. The early midline occipital activity likely represents some of the earliest visual processing within the occipital cortex and may be related to the extraction of nonspecific image properties, like contrast borders (cf. Tarkiainen et al., 2002). Consistent with this view, spatially and temporally similar increases in activation for scrambled images have also been reported (e.g., Halgren, Raji, Marinovic, Jousmäki, & Hari, 2000; Bentin, Allison, Puce, Perez, & McCarthy, 1996; Allison, McCarthy, Nobre, Puce, & Belger, 1994). Moreover, a recent fMRI study showed that BOLD signal strength was directly related to stimulus contrast in V1, V2d, V3d, and V3A (Boynton, Demb, Glover, & Heeger, 1999).

From the midline occipital cortex, activity advanced to the inferior occipito-temporal areas bilaterally, reaching the maximum at about 150 msec after stimulus onset. This activity, especially in the left hemisphere, appears to be related to the processing of letters and/or letter-like objects (Helenius et al., 1999; Tarkiainen et al., 1999) but is nevertheless prelexical as it is insensitive to the distinction between pseudowords versus real words (Salmelin et al., 1996) and even between real words versus consonant strings (present study). The right hemisphere occipito-temporal activity does not typically separate letter strings from strings of geometrical symbols (Tarkiainen et al., 1999) nor words from consonant strings (present study). However, the

right hemisphere response increased when the letters were vertically shifted. An opposite but less robust effect (seen only in criterion search) was observed in the left occipito-temporal cortex where letter shifting reduced the activity. This hemispheric dissociation supports the suggestion that right hemisphere extrastriate areas process the visual stimuli at a more global level, whereas left hemisphere regions participate in more local processing (Fink, Dolan, et al., 1997; Fink, Halligan, et al., 1997). Moreover, it also suggests a lack of shift invariance, inconsistent with the computation of relative letter position.

Broadly, we suggest that our results can be interpreted in the light of Caramazza and Hillis's (1990) model of early processes when we read. Their scheme comprises three levels of information processing: (1) the extraction of retino-centric image features; (2) stimulus-centered letter-shape information; and (3) word-centered grapheme information. The neuroanatomical sites for these stages are not defined by Caramazza and Hillis, but we suggest that, to a first approximation, the patterns of activity we have reported here before 200 msec equate to Caramazza and Hillis's level 1 and perhaps the input to, or early level 2. If so, where is level 3 processing manifested? We speculate that this stage may be reflected in the activation of BA 37 (the visual word form area), which is typically reported in hemodynamic studies of reading, in addition to activation of BA 18/19 (see e.g., Fiez & Petersen, 1998). Our neuromagnetic data show that, up to 200 msec poststimulus, evoked activity in the extrastriate cortex is largely restricted to BA 18/19 (mean Talairach and Tournoux coordinates for the left hemisphere letter-string-specific occipito-temporal activation were -37 , -70 , -12 , Tarkiainen et al., 2002; i.e., posterior fusiform gyrus) with little or no extension into BA 37 territory. Therefore, we suggest that BA 37 activity occurs in a later time window (i.e., after 200 msec) and that—perhaps because of weaker phase-locking to the stimulus presentation—the average evoked neuromagnetic signal was not strong enough to reveal it.

METHODS

Subjects and Stimuli

Ten healthy, right-handed, Finnish-speaking adults (4 women, 6 men) consented to take part in this study. They were all university students or graduates and their ages ranged from 24 to 38 years (mean 28 years 7 months). All subjects had normal or corrected-to-normal visual acuity and their consent was obtained according to the Declaration of Helsinki (BMJ 1991; 302: 1194).

Stimuli comprised 55 four-letter, 55 six-letter, and 55 eight-letter Finnish nouns [e.g., LOMA (holiday), SÄÄTIÖ (foundation), and OPETTAJA (teacher)], as well as 55 six-letter random consonant strings. Mean Log_{10}

word frequencies (Laine & Virtanen, 1999) and word concreteness values were 3.31 ($SD = 0.45$), 3.31 ($SD = 0.38$), 3.30 ($SD = 0.34$) and 3.63 ($SD = 0.70$), 3.78 ($SD = 0.72$), 3.73 ($SD = 0.68$), respectively. A one-factor ANOVA of \log_{10} word frequency and concreteness showed no main effect of string length, $F(2,162) = 0.02$, $p > .5$; $F(2,162) = 0.68$, $p > .5$, respectively. Therefore, the word lists were well controlled with respect to these psycholinguistic variables. Every letter string was presented four times: twice as a linear string, and twice with random shifts of vertical letter position (i.e., up or down one letter height), giving a total of 880 letter strings per experiment. When letter position was modified, the first and last letters were always fixed, only internal letter positions were shifted, and always by an amount equal to the height of one letter. The order of stimulus presentation was randomized. Figure 1 shows examples of the different stimuli.

Procedure

Subjects sat in a dimly lit, magnetically shielded room. Stimulus display was controlled by a Macintosh Quadra 800 and images were back-projected (Electrohome Vista Pro) onto a screen located approximately 1 m in front of the subject. Letter strings appeared on the screen in a centrally placed rectangular patch (subtending approximately 5° by 2°). All images were shown on a large background of uniform gray. The gray level of the background was set to 161 (on a scale 0–255 from black to white), which reduces the eye stress that long viewing of high-contrast grayscale stimuli can induce. Finally, the visual stimulation system we used has a delay of 33 msec but this has been taken account in the results and the latencies we report are relative to the appearance of the image on the screen.

Each experiment involved a 30- to 40-min MEG recording session that was divided into four blocks of 220 trials. There was a rest period of 1–3 min between blocks. During each trial, letter strings appeared for 100 msec followed by a 2000-msec blank interval. Subjects were asked to read words silently to themselves. In order to ensure that they were concentrating on the task, a question mark was presented on 1.5% of trials, prompting subjects to report the word that appeared on the preceding trial. These probe trials were excluded from analysis.

Magnetoencephalography

Neuromagnetic signals, detected with superconductive quantum interference device (SQUID) sensors, are thought to reflect the coherent postsynaptic potentials in large populations ($\sim 10^4$) of pyramidal cells. ECDs can be used as models to derive the locations, orientations, and time-varying strengths of these underlying currents from the distribution of the measured magnetic fields

(for a thorough review of MEG, see, e.g., Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993).

We used a Neuromag Vectorview neuromagnetometer to measure the magnetic fields generated by subjects' cortical activity. This device employs 306 sensors arranged in a helmet-shaped array. We used only the 204 planar gradiometers of the device, which detect maximum signal directly above an activated cortical area.

A head coordinate system was determined which allows the coordinate systems for MEG measurement to be aligned with subjects' MRIs. The head coordinate system is defined in relation to three anatomical landmarks: the nasion and points just anterior to the left and right ear canals.

Prior to MEG measurement, small coils were attached to the subjects' head and the locations of the coils were determined with a 3-D digitiser in the coordinate system defined by the three anatomical landmarks. At the start of MEG measurement, a small electric current was sent to the coils to induce a measurable magnetic field pattern. This allowed the coils to be located with respect to the neuromagnetometer. Since the coil locations were also known in head coordinates, all MEG measurements could be transformed onto the head coordinate system, and co-registered with the subjects' structural MRIs.

Signal Acquisition and Analysis

MEG signals were bandpass filtered between 0.1 and 200 Hz, sampled at 600 Hz and averaged on-line in separate bins, one bin for each stimulus type. Signal averages were calculated for the time window -200 to 800 msec relative to the stimulus onset. Horizontal and vertical electrooculograms were continuously monitored and epochs contaminated by eye blinks and eye movements were excluded from the on-line averages. To achieve an acceptable signal-to-noise ratio, a minimum of 90 trials was averaged for each bin, although typically this total exceeded 100.

Averaged MEG responses were digitally low-pass filtered at 40 Hz. The baseline for the signals was calculated over the period 200 to 0 msec before stimulus onset. For signal analysis, the shape of the conducting volume, that is, the brain, has to be defined (Hämäläinen & Sarvas, 1989). In our studies, we approximated the brain as a spherically symmetric conductor. In each subject, the brain was modeled by a sphere adjusted to the local curvature with the help of the subject's structural MRIs.

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